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INTERMANUAL SOMESTHETIC TRANSFER IN SPLIT-BRAIN RHESUS MONKEYS[1]

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A number of studies have demonstrated that section of the corpus callosum abolishes interhemispheric transfer of memory. Myers (1956) found that cats with mid-line section of the optic chiasm and corpus callosum failed to exhibit interocular transfer of visual discriminations. The animals were trained initially with one eye covered by a rubber mask and were unable to perform the learned discrimination when tested with the untrained eye. Nor was any saving apparent in relearning with the second eye under these conditions (Sperry, Stamm, & Miner, 1956). By contrast, control animals with either callosum or chiasm section alone showed excellent interocular transfer. More recently, Sperry (1958) and Downer (1958) have independently reported the same effect in the monkey. Section of either the callosum or the chiasm alone did not block interocular transfer of learned visual discriminations, while section of both resulted in the absence of transfer of these discriminations to the untrained eye. Further, diametrically opposed discriminations could be learned with the separate eyes in the split-brain cat and monkey with no apparent cross-interference between the hemispheres (Myers, 1956; Sperry, 1958).

Since the great majority of cutaneous and proprioceptive fibers project to the contralateral hemisphere, it might be expected that section of the corpus callosum would block also the intermanual transfer of somesthetic discriminations. In 1924 Bykov had reported that section of callosum in dogs tended to prevent the usual contralateral transfer of cutaneous conditioning of salivary reflexes. Stamm and Sperry (1957) recently demonstrated an absence of interpaw transfer of somesthetic discrimination in cats in which the callosum had previously been sectioned. These animals were trained with one paw to push one of two differently cued pedals on the basis of touch alone. They showed no savings when tested for knowledge of these learned somesthetic discriminations on the second paw, as opposed to controls which showed high savings. The motor aspects of the pedal-pushing habit in this study likewise failed to show transfer in the callosum-sectioned cats. Myers[2] too has recently observed an absence of intermanual motor transfer of a latchbox problem in chimpanzees following section of the corpus callosum.

On the other hand, Sperry (1958) has reported a case of high-level intermanual transfer of somesthetic discriminations in a chiasm- and callosum-sectioned monkey, and Smith (1952) had earlier found indications of intermanual transfer of a stylus-maze task in callosum-sectioned humans. The present study is an attempt to gain further information on these points relating to intermanual transfer following section of the corpus callosum.

METHOD

Subjects

Seven rhesus monkeys were used, three normals and four callosum-sectioned. The anterior and hippocampal commissures were also sectioned along with the corpus callosum in all four experimental cases. At the start of the experiment the three normals as well as CLR and CLK of the experimental group were adolescent and experimentally naive, weighing an average of about 7 lb. Subjects CVN and BRN were somewhat older, weighing about 12 lb., and had also undergone prior section of the crossover fibers of the optic nerve at the chiasm in addition to the mid-line section of the corpus callosum. The latter two animals had been *S*s in a previous study of interocular transfer of visually learned discriminations. No significant effects were noted which could be attributed to differences in age and prior experience of animals in the experimental group.

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[2] Myers, R. E. Personal communication, 1959.

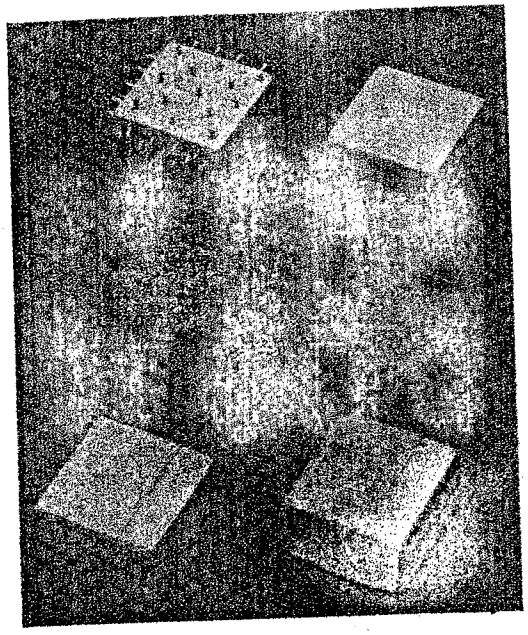

FIG. 1. Test objects used for somesthetic discrimination learning.

Apparatus

Monkeys were trained in a test cage, the front of which contained a barrier with an adjustable opening wide enough for the animals to reach through. Two eye holes allowed vision to right or left eye, both, or neither. The test objects were presented in pairs covering food wells and so placed in front of the arm opening that the monkey could feel, but not see, the discriminanda. A sliding barrier permitted *E* to restrict the monkey to use of one or the other hand. A total of three pairs of discriminanda were used. In the initial tactile problem (rough vs. smooth) the objects were two square blocks of wood 4.5 by 4.5 and 1.4 cm. high, one of which was smooth, the other covered by partially inserted $\frac{3}{8}$-in. O screws. The two subsequent problems were high vs. low (tape-covered square blocks of wood of the same size base as the preceding, but of different heights, 2.5 and .5 cm high, respectively) and a cone vs. tetrahedron equivalent in volume and of the same base size as the others. The three pairs of test objects are pictured in Figure 1.

Surgery

The corpus callosum, psalterium, and anterior commissure were sectioned by removing on one side a large skull plate that extended about 3 mm. across the midline. The exposed hemisphere was retracted slightly to expose the callosum. This and the subsequent cutting procedures and other detailed aspects of the surgery were all carried out with the aid of a binocular dissecting microscope. Section of the optic chiasma in CVN and BRN was effected via a dorsal approach through the sectioned corpus callosum.

Procedure

Problem I, direct testing. The monkeys were first taught to reach out of the test cage and remove food from the open wells. The wells were then gradually covered by the objects to be used in the initial tactile problem (rough vs. smooth), and one of the two dissimilar cues was consistently rewarded irrespective of its position. Next, the eye holes were gradually narrowed until the animal was working entirely without vision. The two test objects were alternated in accordance with Gellermann's (1933) principles except when a position habit developed. If the monkey consistently chose the right or left object for as many as 10 successive trials, the correct discrimination was placed on the nonpreferred side until 3 successive correct responses were made. Subjects were trained on this preliminary discrimination until they responded correctly 17 out of 20 successive trials. The habit was then stabilized by overtraining a minimum of 400 trials or as many as were required for initial learning if this exceeded 400. Transfer testing and retraining with the second hand were started without vision as soon as overtraining was completed on the first hand. Learning criterion and amount of overtraining were determined in the same way for the second hand.

Because of the preliminary nature of this first problem, savings scores tend to be confounded by nonspecific effects. In most cases the number of trials to criterion with the first hand is somewhat arbitrary. For example, both BRN and CVN had been previously trained on a number of visual problems, and there was an initial difficulty in training these animals to work without vision. Therefore, transfer is reported in terms of number and percentage correct in the first 40 trials for the second hand, rather than savings percentage.

In the initial discrimination problem it was possible to observe the emergence of a "testing habit" after complete restriction of vision, i.e., the animal learned to feel both patterns before selecting one or the other. A fully trained monkey would typically reach out and touch one object of the pair; if it were the correct one, *S* would remove it; if not, *S* would go to the second side. This touching of both patterns before selecting one or the other was scored as tactile testing. Since the animals tended consistently to test the same side first on each trial, and since this first side was correct five times in any block of 10 trials, a criterion for establishment of the tactile-testing habit was set at five tactile testings in 10 successive trials. The numbers of trials required to reach this criterion were recorded starting at the point where vision was excluded.

Problems II and III, reversal and rereversal testing. After completion of training on the initial tactile problem with both hands, the monkeys were trained on two succeeding tactile discriminations (high vs. low and cone vs. tetrahedron). The general procedure was the same as for the initial problem except for the following. In these latter problems the tests for transfer to the untrained hand were conducted with the stimulus values reversed. Thus, e.g., if the left hand had been trained to the high block as positive, the low block would be positive for the right hand. Accordingly, transfer of the specific sensory information would be evident in a tendency to select the previously positive

stimulus, producing an initial score close to zero correct or significantly below chance. In the absence of somesthetic transfer, the monkey would be expected to perform at a chance (50%) level initially. After completion of reversal training on the second hand, all cases were retested on the first hand with original stimulus values; i.e., the discriminanda were rereversed. If the reversal had transferred, animals again would be expected to perform initially near zero correct. In the absence of transfer the performance should be carried over from the initial learning and approach 100%. This provided a second measurement of the extent of somesthetic transfer in experimental and control animals.

Results

Transfer of Tactile Testing Habit

Table 1 presents the results of the tests for transfer of the tactile testing habit on the initial problem with the first and second hands for the three normal and three of the callosum-sectioned animals. (Monkey CVN is not included since she had received some previous training on a visuotactile problem and had learned tactile testing in the course of it.) In general, training was begun with the nonpreferred hand. Since all the present group tended to prefer the right hand, training was begun with the left. Note that in callosum-sectioned as well as control animals this testing component of the learning transferred consistently to the untrained paw.

Sensory Transfer: Direct

Table 2 shows the results obtained in the normal and callosum-sectioned animals in the tests for transfer of the initial tactile problem. The performance in the first 40 trials is given and also the percentage of savings in relearning the problem with the second hand. Subjects BRN and CVN performed at a chance level in the first 40 trials with the second hand, whereas CLK and CLR were significantly above chance. Curiously, however, CLK's level of performance dropped back to a chance level within 100 trials, and in spite of the reinforcement *S* did not again reach criterion on the second hand until 550 trials. CLR, one of the callosum-sectioned animals, began at a high level of performance and maintained it, as did KNG and HRV of the normal group. JLS, although beginning at a poorer level of performance, nevertheless reached criterion within 50 trials and maintained a high level of performance. Thus, although there tended to be a lack of intermanual sensory transfer in the callosum-sectioned cases, CLR was an exception in that it showed definite and persisting evidence of transfer.

TABLE 1

Tactile Testing Habit: Number of Trials Required To Reach Criterion

Animal	Hand 1	Hand 2	% Savings
Normal			
HRV	L 410	R 0	100
KNG	L 170	R 0	100
JLS	L 200	R 60	70
Callosum-Sectioned			
BRN	L 630	R 0	100
CLR	L 330	R 0	100
CLK	L 270	R 0	100

TABLE 2

Problem I: Number and Percentage of Correct Responses in First 40 Trials with Untrained Hand

Animal	Hand	Correct	% Correct
Normal			
HRV	R	34	85**
KNG	R	39	98**
JLS	R	25	62
Mean		33	82
Callosum-Sectioned			
CVN	R	18	45
BRN	R	18	45
CLK	R	33	82**
CLR	R	33	82**
Mean		26	64

** Significantly above chance. $p < .01$

Reversal Tests

The performance with the second hand on Problem I was facilitated to a considerable, though unmeasurable, extent by transfer of the motor testing habit and possibly other nonspecific aspects of the trained performance. In order to separate "transfer" from "preference" effects and the specific sensory from other components of the learning, reversal testing was employed in the next two problems. Transfer of the sensory discrimination under

TABLE 3

PROBLEMS II AND III: TEST OF SECOND HAND FOR TRANSFER (REVERSAL). PERCENTAGE CORRECT RESPONSES IN FIRST 40 TRIALS
(H-L = High vs. Low; C-T = Cone vs. Tetrahedron)

Animal	Problem	Hand	No. Correct	% Correct
		Normal		
HRV	I: H-L	L	2	5[b]
	II: C-T	R	15	38
KNG	I: C-T	L	3	8[b]
	II: H-L	L	10	25[b]
JLS	I: H-L	L	2	5[b]
Mean			6	16
		Callosum-Sectioned		
CVN	I: H-L	R	12	30[a]
	II: C-T	L	1	2[b]
BRN	I: H-L	R	23	58
	II: C-T	L	18	45
CLR	I: H-L	L	31	78[d]
	II: C-T	R	20	50
CLK	I: H-L	L	15	38
	II: C-T	L	31	78[d]
Mean			19	47

[a] Significantly below chance; $p < .05$.
[b] Significantly below chance; $p < .01$.
[d] Significantly above chance; $p < .01$.

TABLE 4

PROBLEMS II AND III: RETEST OF ORIGINAL HAND AFTER REVERSAL TRAINING ON SECOND HAND PERCENTAGE CORRECT RESPONSES IN FIRST 40 TRIALS
(H-L = High vs. Low; C-T = Cone vs. Tetrahedron)

Animal	Problem	Hand	No. Correct	% Correct
		Normal		
HRV	I: H-L	R	8	20[b]
	II: C-T	L	5	12[b]
KNG	I: C-T	R	6	15[b]
	II: H-L	R	26	65
JLS	I: H-L	R	5	12[b]
Mean			10	25
		Callosum-Sectioned		
CVN	I: H-L	L	39	98[d]
	II: C-T	R	28	72[c]
BRN	I: H-L	L	39	98[d]
	II: C-T	R	25	62
CLR	I: H-L	R	40	100[d]
	II: C-T	L	39	98[d]
CLK	I: H-L	R	40	100[d]
	II: C-T	R	38	95[d]
Mean			36	90

[a] Significantly below chance; $p < .05$.
[b] Significantly below chance; $p < .01$.
[c] Significantly above chance; $p < .05$.
[d] Significantly above chance; $p < .01$.

these conditions would show up as an initial tendency to select the incorrect stimulus.

Table 3 summarizes the transfer scores of all seven animals on the first reversal of each problem. (After completion of training on H-L, JLS developed an infection and had to be sacrificed.) It is apparent that there is strong sensory transfer for the normal controls (significantly less than chance performance), whereas among the callosum-sectioned group there was definite transfer in only one of the four cases, CVN, and in this case transfer occurred on both problems. The high positive scores for CLR and CLK, which were maintained, show that a spontaneous preference, if reinforced, could simulate transfer with direct testing. Monkey CVN's persistent choice of the unrewarded stimulus, however, can hardly be ascribed to a preference effect.

Rereversal Tests

Table 4 shows the data for rereversal testing, i.e., retesting the first hand with original stimulus values after the reversal tests with the second hand. In seven of eight tests the callosum-sectioned animals were significantly above the 50% chance level. Even in those cases that exhibited transfer in other instances (CVN, CLR) the reversed learning failed to transfer. On the other hand, the normal controls in all but one case are well below chance level of performance. It is noteworthy that KNG, although unoperated, began to show signs of independence of the two hemispheres, similar to our callosum-sectioned cases.

Specific Motor Transfer (Finger Movements)

Quantitative data were not obtained for specific motor transfer, but in addition to the direct observations we have motion-picture records of the transfer tests on three callosum-sectioned animals (BRN, CVN, and CLR) and one normal control (HRV). There was marked individual variation in the pattern of finger movements applied by the different monkeys in learning the same problem. Our one control case used an almost identical pattern of finger movements with its first and second hand. By

contrast all three callosum-sectioned animals shifted to a different pattern of finger movements in testing the patterns with the second hand. Even CVN, which showed sensory transfer on reversal testing, used rather different finger movements in testing high vs. low with the second hand.

Transfer Correlated with Cerebral Damage

The one callosum-sectioned monkey that exhibited strong transfer (CVN) with reversal testing differed from the others in having shown a marked impairment in the use of the left hand subsequent to its operation in which the commissures and optic chiasm were sectioned. The partial paralysis reached a peak on the fourth day after the operation and then gradually disappeared in succeeding weeks. Post-mortem examination confirmed that the right somatic cortex (the side exposed in surgery) had undergone considerable softening and degeneration extending into the arm areas. It seemed possible that the unilateral cortical damage in this case may have tended to force the learning to occur predominantly on the undamaged side even when the ipsilateral hand was used.

Accordingly, an attempt was made in a second case (CLR) to induce transfer intentionally in this way by making a near-total removal of the right sensorimotor cortex. In two previous problems (H-L, C-T) this same animal had shown no intermanual transfer (Tables 3 and 4). A new discrimination involving differently shaped objects (small Bunsen burner vs. electrical plug) was trained after the operation to the hand ipsilateral to the cortical removal. In this, CLR, like CVN, exhibited good transfer on reversal testing.

Anatomical Verification

At present the brains of two of the four animals in the callosum-sectioned group (BRN and CVN) have been examined, and all the intended sections of optic chiasm, corpus callosum, and anterior and hippocampal commissures were found to be complete. The remaining two experimental animals (CLK and CLR) are presently *S*s in another experiment, and description of their sections will be reported in a subsequent publication.

Discussion

The foregoing analysis of intermanual transfer of learned somesthetic discriminations indicates that different components of the learning complex differ in the degree to which they are subject to transfer. In all cases the general, gross aspects of the testing procedure and orientation to the training apparatus, acquired during learning with the first hand, transferred with little or no loss to the performance with the untrained hand.

The specific ability to select the correct stimulus transferred in the normal group at a high level (6 out of 8 tests, Tables 2 and 3), but failed to transfer in the majority of tests (8 out of 12, Tables 2 and 3) in the callosum-sectioned cases. We may infer from this that section of the callosum interferes with and may block completely the normal contralateral transfer of somesthetic discrimination learning in *Macaca mulatta*. This result is in line with earlier findings on the cat (Stamm & Sperry, 1957).

However, as we have noted, in a minority of the tests there appeared to be definite transfer of the specific sensory components of the habit. From this and an earlier observation (Sperry, 1958), it would appear that an extracallosal mechanism or apparatus for intermanual transfer is present in the rhesus monkey. It seems likely that the homolateral somesthetic projection system is responsible either for establishing traces bilaterally during learning, or for making the primary unilateral trace system available to the untrained hand. Thus, the apparent forcing of transfer in CVN and CLR by damage to the somatic cortex on one side suggests that traces may be formed directly in the homolateral hemisphere during manual learning or else that a dominant trace system formed originally on the contralateral side can be used by the second as well as the first hand. The interpretation is complicated, however, by the further finding that the reversal learning failed to transfer in either CVN or CLR. Whether the extra-callosal apparatus for intermanual transfer will be effectively used in any given learning situation probably depends on a variety of factors such as the degree of unilateral cerebral dominance, the nature and difficulty of the problem, and

possibly the training procedure and amount of overtraining.

It should be emphasized perhaps that the occurrence of intermanual transfer is not in itself any contradiction of the more general conclusion that section of the callosum and anterior commissure effectively separates the learning and memory processes of the two hemispheres. Even where somesthetic discrimination transfers, the learning process of each hemisphere presumably proceeds independently in the absence of the neocortical commissures.

In tests for transfer of the reversed habit of the second hand back to the first hand, the controls showed high-level transfer whereas the callosum-sectioned monkeys failed to transfer. The presence of reversal transfer in the controls attests to the high development of the callosal system in the monkey as compared with the cat. In the cat the habit of the directly trained hemisphere tends to be decidedly stronger than that established in the opposite hemisphere via the callosum (Myers & Sperry, 1958). This difference seems to be reduced in the monkey.

Motor Transfer

Our observations on the intermanual transfer of specific finger movements supported by cinematography indicated good transfer in the controls and lack of transfer in the callosum-sectioned cases. This is in line with R. E. Myers' unpublished data for the chimpanzee. It contrasts markedly with the consistent transfer of the more gross phases of the motor pattern, including arm movement. The difference here may depend in part on the degree to which the movement in question is unilaterally cued. The more general phases of the learning may not be unilaterally cued nor unilaterally regulated, and to that extent their transfer would not be unexpected. The more closely the details of motor coordination are tied to the sensory discrimination, the more likely is their transfer to run in parallel. In this regard it is particularly interesting that the specific motor carry-over should fail even when the discrimination itself transferred in CVN. However, further study is needed to specify more thoroughly the presence and degree of intermanual motor transfer.

Summary

Analysis of intermanual transfer of learned somesthetic discriminations in split-brain monkeys showed that section of the callosum effectively blocked the normally strong transfer from the trained to the untrained hand in the majority of tests. However, good transfer occurred in the absence of the callosum in a small minority of the tests. When training with the second hand was the reverse of that with the first hand, good transfer of the reversed habit back to the first hand prevailed among the controls but was consistently absent throughout the experimental group. The general testing procedure of reaching out and feeling the two test objects before selecting transferred consistently in the split-brain group, whereas the specific pattern of finger movements used in testing failed to transfer.

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